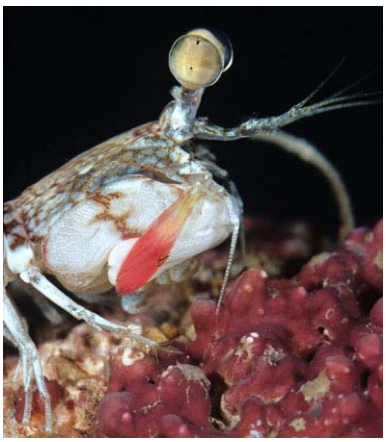
Final Report for AOARD / AFOSR post-doctoral project

***Project title**: Processing of visual information in mantis shrimps*



Subject: Processing of visual information in mantis shrimps
Grant number: FA5209-04-P-0395
Applicants: Justin Marshall, Sonja Kleinlogel
Location: The University of Queensland, Australia
Due date: August 2006

Stomatopod crustaceans have the most complex visual system, at photoreceptor level, of any animal yet known and this project aims to learn from this evolved elegance and eventually look towards biomimetic solutions for visualising with man-made imaging systems in a number of environments.

Due to exciting findings along the way the project has departed from original aims to an extent and has largely concentrated on polarisation vision in stomatopods (see updated aims attached). We are amazed by some of the outcomes of this work, much of which has been done in close collaboration with Tom Cronin and his lab and Roy Caldwell in the USA.

During the two years of this project we addressed the following questions:

1) Do stomatopods possess circular polarization sensitive photoreceptors in mid-band rows 5&6?
2) Do the distally placed R8 cells of mid-band rows 5&6 act as quarter-wave retarders to convert circularly polarized light into linearly polarized light so it can be analyzed by the R1-R7 cells beneath?
3) What are the physiological properties (spectral and polarization sensitivities) of all photoreceptors within the stomatopod retina?
4) What is the anatomy, connectivity and physiology of visual interneurons within the three optic neuropils, the lamina, the medulla and the lobula?

Summary of Achievements:

1) We have shown, with multiple lines of evidence (structural, optical, electrophysiological and behavioural), that the R1-R7 photoreceptors within the stomatopod's mid-band rows 5&6 are sensitive to circular polarized light. This is the first time that circular polarization sensitivity has been shown in any animal.
2) The overlying R8 cells within these two mid-band rows act as quarter-wave retarders in the spectral range the R1-R7 cells are sensitive to. Furthermore we found that the R8 cells of mid-band rows 5&6 have a dual function in two separate spectral bands; besides being quarter-wave retarders in the green they are themselves linear polarization sensitive photoreceptors in the ultraviolet.
3) The polarization and spectral sensitivities of all photoreceptors within the retina of several species have been measured and each cell type has been identified by subsequent intracellular dye-injection.

Report Documentation Page

Form Approved
OMB No. 0704-0188

1. REPORT DATE	2. REPORT TYPE	3. DATES COVERED
05 JUN 2007	**FInal**	**01-09-2004 to 01-08-2006**

4. TITLE AND SUBTITLE **Processing of Visual Information in Mantis Shrimp**	5a. CONTRACT NUMBER **FA520905P0273**
	5b. GRANT NUMBER
	5c. PROGRAM ELEMENT NUMBER
6. AUTHOR(S) **Justin Marshall**	5d. PROJECT NUMBER
	5e. TASK NUMBER
	5f. WORK UNIT NUMBER
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) **The University of Queensland,St. Lucia,Brisbane, Queensland 4072,Australia,AU,4072**	8. PERFORMING ORGANIZATION REPORT NUMBER **N/A**
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) **AOARD, UNIT 45002, APO, AP, 96337-5002**	10. SPONSOR/MONITOR'S ACRONYM(S) **AOARD**
	11. SPONSOR/MONITOR'S REPORT NUMBER(S) **AOARD-054006**

12. DISTRIBUTION/AVAILABILITY STATEMENT
Approved for public release; distribution unlimited

13. SUPPLEMENTARY NOTES

14. ABSTRACT
Report of a 3 year investigation into the physiological structure of the mantis shrimp eye. This creature has the most advanced and most complex eye of any creature in nature, with many band-pass elements, including those outside of human viewing spectra. It also can see polarized light (linear and circular, both directions)

15. SUBJECT TERMS
Biomimetics, Biosensors, Vision

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT	b. ABSTRACT	c. THIS PAGE			
unclassified	**unclassified**	**unclassified**	**Same as Report (SAR)**	**14**	

4) The Golgi staining method is renowned to be difficult to use successfully on crustacean tissue. We developed a Golgi staining method specifically for stomatopod eyes in order to investigate the detailed anatomy of visual interneurons. Anatomical findings from this and other techniques are summarised below

Bibliography of publications

Kleinlogel S, Marshall NJ. Photoreceptor projection and termination pattern in the lamina of gonodactyloid stomatopods (mantis shrimp). *Cell Tissue Res* **321**, 273-284 (2005).

Kleinlogel S, Marshall NJ. Electrophysiological evidence for linear polarization sensitivity in the compound eyes of the stomaopod crustacean *Gonodactylus chiragra*. *J Exp Biol **209**, 4262-4272.*

Marshall J, Cronin T, Kleinlogel S. A review of stomatopod eye structure and function. In: Evolution of arthropod visual systems. Eds: Steinbrecht and Strausfeld. *Accepted*.

In Preparation

Kleinlogel S and Chiou T-H, Caldwell RL, Cronin TW, Marshall NJ. Circular polarization vision in gonodactyloid stomatopods.

Kleinlogel S, White AG, Marshall NJ. Multidimensional polarization vision in a stomatopod crustacean, *Odontodactylus scyllarus* (Linnaeus).

Kleinlogel S, Marshall NJ. A dual role of an ultraviolet sensitive photoreceptor in a stomatopod crustacean: linear polarization receptor and quarter wave retarder.

Kleinlogel S, Marshall NJ. 16 spectral sensitivities in the eyes of a gonodactyloid stomatopod crustacean: an electrophysiological study.

Meeting abstracts

Kleinlogel S, Marshall NJ. (2005) 12 spectral and 4 polarization sensitivities within a crustacean eye. Gordon Conference Neuroethology: Behavior, Evolution & Neurobiology, Oxford, UK.

Kleinlogel S, Marshall NJ. (2005) A crustacean retina with 12 spectral and 4 polarization sensitivities. SfN Conference, Washington DC, USA.

Achievements

General Comments

This study has been undertaken on several gonodactyloid stomatopod species: *G. chiragra, G. smithii, H. glyptocercus, H. trispinosa* and *O. scyllarus.* The data presented here is mainly from *O. scyllarus* and *G.smithii* if not stated otherwise, both of which possess circular polarization sensitivity.
Specific discoveries are detailed in the figures, figure legends and publications.

Collaborators

a) Circular polarization vision project
Prof. TW Cronin and PhD student Chiou T-H (University of Maryland, USA), Prof. RL Caldwell (Berkley University, USA), Prof. A White (University of Queensland, Australia)
b) Neuroanatomy and recordings from visual interneurons
Prof. N Strausfeld and Dr. J Douglass (University of Arizona, USA)

A) The circular polarization sensitive photoreceptors of mid-band rows 5&6

With intracellular recordings combined with dye-injections (Lucifer yellow and Ethidium bromide) we could show that, as hypothesized, mid-band row 5&6 R1-R7 photoreceptors of the species *O. scyllarus* and *G. smithii* are sensitive to circular polarised light. All of the cells showed a high sensitivity to circular polarized light of 8.24 ± 3.12 (mean ± s.d.) and negligible if any sensitivity to linear polarized light (Fig. 1). We used an achromatic polarization filter in combination with an achromatic quarter-wave plate to produce circular polarized light. Subsequent calculations of the Stokes vector from the three Stokes parameters showed that R1-R7 in mid-band rows 5&6 are exclusively sensitive to circular polarized light (92%) and not to linear or elliptical polarized light.

B) The linear polarization sensitive photoreceptors of the hemispheres

The R1-R7 photoreceptors within both, the dorsal and the ventral hemispheres, are sensitive to 4 e-vector directions of linear polarized light. In *O. scyllarus* the e-vector directions of maximal sensitivity are at 30˚ and 120˚ in the dorsal hemisphere and 75˚ and 165˚ in the ventral hemisphere (in a left eye with 0˚:= vertical).

All hemispheric receptors showed a high sensitivity to linear polarized light of 8.4 ± 2.6 (mean ± s.d.). Although most of these photoreceptors were insensitive to circular polarized light, a few cells showed a low circular polarization sensitivity of ≤ 1.6 (Figure 2). In order to determine if the cells were sensitive to elliptical light rather than linear polarized light, we calculated the Stokes vector from the Stokes parameters. The results showed that hemispheric cells are exclusively sensitive to linear polarized light (86%).

C) Dual functionality of the R8 cells of mid-band rows 5&6 in two spectral wavebands

a) Quarter-wave retarder in the green spectral band:

The distally placed R8 cells within mid-band rows 5&6 act as quarter-wave retarders in the spectral band around 550 nm, the wavelength the R1-R7 cells are the most sensitive to, and they convert circular polarized light to linear polarized light so it can be analysed by the R1-R7 cells beneath. The R8 cells produce parallel microvilli which are arranged at ± 45˚ to the microvilli of the R1-R7 cells (Marshall et al., 1991). Our results have shown that the R8 cells possess exactly the right birefringence and length to act as quarter wave retarders (Fig. 5). In electrophysiological recordings the R1-R7 cells did not show any remaining linear polarization sensitivity, and the photoreceptors R1-R7 with their microvilli arranged at 45˚ to the microvillar (optical) axis of the overlying R8 cells were more sensitive to right-handed circular polarized light whereas the photoreceptors R1-R7 with their microvilli arranged at -45˚ to the microvillar (optical) axis of the overlying R8 cell were more sensitive to left-handed circular polarized light (in a left eye) (Fig. 4). This is only so if the R8 cell acts as a quarter-wave retarder.

b) Linear polarization receptor in the ultraviolet

R8 cells in stomatopods are spectrally sensitive to ultraviolet light (Marshall and Oberwinkler, 1999). Only the R8 cells of mid-band rows 5&6 possess parallel microvilli and it was therefore predicted that they are sensitive to linear polarized light with an e-vector oriented parallel to their microvillar axis (Marshall et al., 1991). Row 5 R8 cells possess horizontally arranged microvilli (parallel to the equator of the eye) whereas row 6 R8 cells form vertically arranged microvilli (orthogonal to the equator of the eye). This 90˚ rotation of photoreceptor arrangement in row 6 compared to row 5 may have evolved to form a linear polarization opponency channel in the UV comparing row 6 R8 cell input to row 5 R8 cell input (Kleinlogel and Marshall, 2005). We used an UV linear polarization filter (HNP'B, Polaroid Company) for electrophysiological recordings from R8 cells and our results corroborate the hypothesis that rows 5 and 6 R8 cells are linear polarization receptors in the UV. Row 5 R8 cells were sensitive to horizontal e-vector orientation and row 6 R8 cells to vertical e-vector orientation (Fig. 6). Row 5&6 R8 cells showed an average sensitivity to linear polarized light of 2.73±0.39 (mean ± s.d.) when activated with monochromatic light at their peak wavelength of 331 nm. None of the cells was sensitive to circular polarized UV light. The lower linear polarization sensitivity value compared to hemispheric receptors is probably due to increased self-screening within the rather long (150 µm) rhabdom of the R8 cell.

D) Prediction of how polarisation information is combined / analysed

The assumption is that stomatopods can see any modality of polarized light by "extracting" the 3 Stokes Parameters from the simultaneous inputs of the 4 linear polarization receptors of the hemispheres and the 2 circular polarization channels of mid-band rows 5&6. The requirements for this are: 1) simultaneous input from all 6 polarization channels which is achieved by overlapping visual fields 2) homochromatic polarization channels 3) the first step of polarization processing is an opponency mechanism, which has been suggested from the neural wiring within the first visual neuropil, the lamina (Kleinlogel and Marshall, 2005). The Stokes parameters determine all three parameters of polarized light: overall intensity, the degree of polarization and the direction of the e-vector. Unpolarised background substraction could increase visibility and contrast underwater even more.

E) Neural wiring of polarization sensitive photoreceptors

The two photoreceptor groups within each ommatidium of the hemispheres and mid-band rows 5&6 which form orthogonal microvilli and are therefore sensitive to perpendicular e-vector directions of light terminate in different plexiform layers within the first optic neuropil, the lamina (Kleinlogel and Marshall, 2005). In mid-band rows 5&6, Group I (R1, R4, R5) photoreceptor axons of both rows terminate in the external lamina plexiform layer whereas Group II (R2, R3, R6, R7) photoreceptor axons terminate in the inner lamina plexiform layer. This finding was initially a surprise as we assumed that mid-band rows 5&6 R1-R7 cells were sensitive to linear polarized light. Because the cell arrangement in row 6 is rotated 90˚ compared to row 5 (Figure 4B), photoreceptors which are sensitive to orthogonal e-vector directions of light would terminate within the same lamina plexiform layer. This conundrum has now been solved knowing that the R1-R7 cells of mid-band rows 5&6 are sensitive to circular polarized light. The same cell groups within both rows are sensitive to the same handedness of circular polarized light (in a left eye: R1, R4, R5 to left-handed circular polarized light and R2, R3, R6, R7 to right-handed circular polarized light). Uniform polarization information channels are therefore maintained within the lamina (Figure 4).

F) The polarization vision system of G. chiragra

For a detailed description see (Kleinlogel and Marshall, 2006)

Gonodactylus chiragra lacks circular polarization sensitive photoreceptors within mid-band rows 5&6. Instead the R1-R7 cells within mid-band rows 5&6 are highly sensitive to linear polarized light of two orthogonal directions (PS = 6.7 ± 1.3). They possess narrow spectral sensitivity functions peaking at 565 nm in contrast to the broad spectral sensitivities measured in *G. smithii* and *O. scyllarus* (Figure 3). Unexpectedly, photoreceptors within the distal rhabdomal tier of mid-band row 2 (2D) also possess highly sensitive linear polarization receptors, which are in their spectral and polarization characteristics similar to the receptors of MB rows 5 and 6. The hemispheric R1-R7 receptors of *Gonodactylus chiragra* possess a lower linear polarization sensitivity than in *G. smithii* and *O. scyllarus* (PS = 3.8 ± 1.6), but they also have broad spectral sensitivity functions peaking at around 500 nm. *Gonodactylus chiragra* is rather exceptional as this species lacks coloured and polarized body markings.

G) Behavioural experiments investigating circular polarization vision in O. scyllarus

Male and female *O. scyllarus* were trained by operant conditioning to feed from cylindrical containers reflecting a particular handedness of circular polarized light. The behavioural experiments have been performed in both, our lab and Tom Cronin's lab. The data from different individuals vary greatly and show rather low significance levels. We are presently trying to collect more convincing data.

H) Circular polarization reflection from the carapace of stomatopods

The keel of *Gonodactylus cultifer* and the spines of the telson of *O. scyllaurs* both reflect circular polarized light. However, both structures also strongly reflect linear polarized light. An interesting question for the future would be if stomatopods also use circular polarized body markings for signalling as they do use linear polarized body markings (see previous project 'Multidimensional Polarisation vision in Mantis Shrimps and other animals'). For detailed information contact Roy Caldwell and Tom Cronin.

I) A total of 16 spectral sensitivities

No other animal is known with such an enormous variety of spectral receptors, particularly that the spectral range from 300 nm to 730 nm could be covered by only 4 photoreceptors.

Our results comply with previous computations from microspectrophotometric spectral data taking into account filtering effects within the cornea, crystalline cones and the rhabdom itself (Cronin et al., 2000). Here we comment on the spectral sensitivities found in the eye of *O. scyllarus*. In general the spectral sensitivities found in other gonodactyloid species (*G. chiragra, O. scyllarus, G. smithii, H. trispinosa, H, glyptocercus*) are very similar (exception see F).

The R1-R7 cells within the 'colour vision system' of mid-band rows 1-4 form a 2-tiered rhabdom and each tier is sensitive to a different wavelength of light (8 in total) (Figure 7A). Notice the double-peaked sensitivity of cells within rhabdom 4D. This row shows a green fluorescence under UV-excitation and the emitted green light may activate the R1-R7 cells under ultraviolet illumination.

Hemispheric and mid-band rows 5&6 R1-R7 photoreceptors have very similar spectral sensitivities peaking around 550 nm (Figure 3). The main difference between the spectral sensitivity functions is the UV-peak, which is only found in hemispheric receptors. This is due to either 1) the increased filtering effect of the elongated R8 rhabdom in mid-band rows 5&6 and the extremely narrow and short-wavelength shifted sensitivity of hemispheric R8 cells (see Figure 7B) or 2) electrical coupling between the R8 cells (UV-sensitive) and the R1-R7 cells (green sensitive) in hemispheric ommatidia. Electrical coupling may here be advantageous to achieve high acuity and contrast.

We found 6 different spectral sensitivity functions peaking in the ultraviolet between 300 nm and 400 nm. All UV-sensitive cells were R8 cells. Unfortunately the detailed anatomy of the connectivity of R8 cells from neighbouring mid-band rows in the medulla externa is yet missing, as it would give clues if dichromatic UV-channels within mid-band rows 1-4 (colour vision rows) and a 2-dimensional polarization vision system in the UV-spectral band within mid-band rows 5&6 (polarization vision rows) existed. Some evidence for lateral connections of neighbouring R8 cell terminals within the medulla externa exist (Kleinlogel and Marshall, 2005) and double-peaked sensitivities were recorded quite frequently from R8 receptors which are an indication of electrical coupling between R8 cells from neighbouring mid-band rows (Figure 7B).

J) Neuroanatomy of the optic neuropils

During a visit to Prof. N. Strausfeld's laboratory (Division of Neurobiology, University of Arizona, USA) in October/November 2005 and January 2006 we developed a Golgi-staining-method (Cajal and Sanchez, 1915) for stomatopod tissue to explore the structure and connectivity of the visual neuropils. We also used the Bodian staining method for comparative gross anatomy. The data has yet to be analysed in detail, but it appears that despite the general arthropod neuroanatomy, including a lobula plate (Strausfeld, 2005), the number of neurons in stomatopods is much greater than in insects and crabs and some appear to be unique to stomatopods.

In collaboration with Prof. N. Strausfeld and Dr. J. Douglass of the University of Arizona (USA) we also developed a preparation to record electrophsyiologically from visual interneurons within the optic neuropils (See mid-year report February 2006). This project was to be continued in collaboration with Dr. David O'Carroll (University of Adelaide), but unfortunately the time did not allow for this.

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Specific results

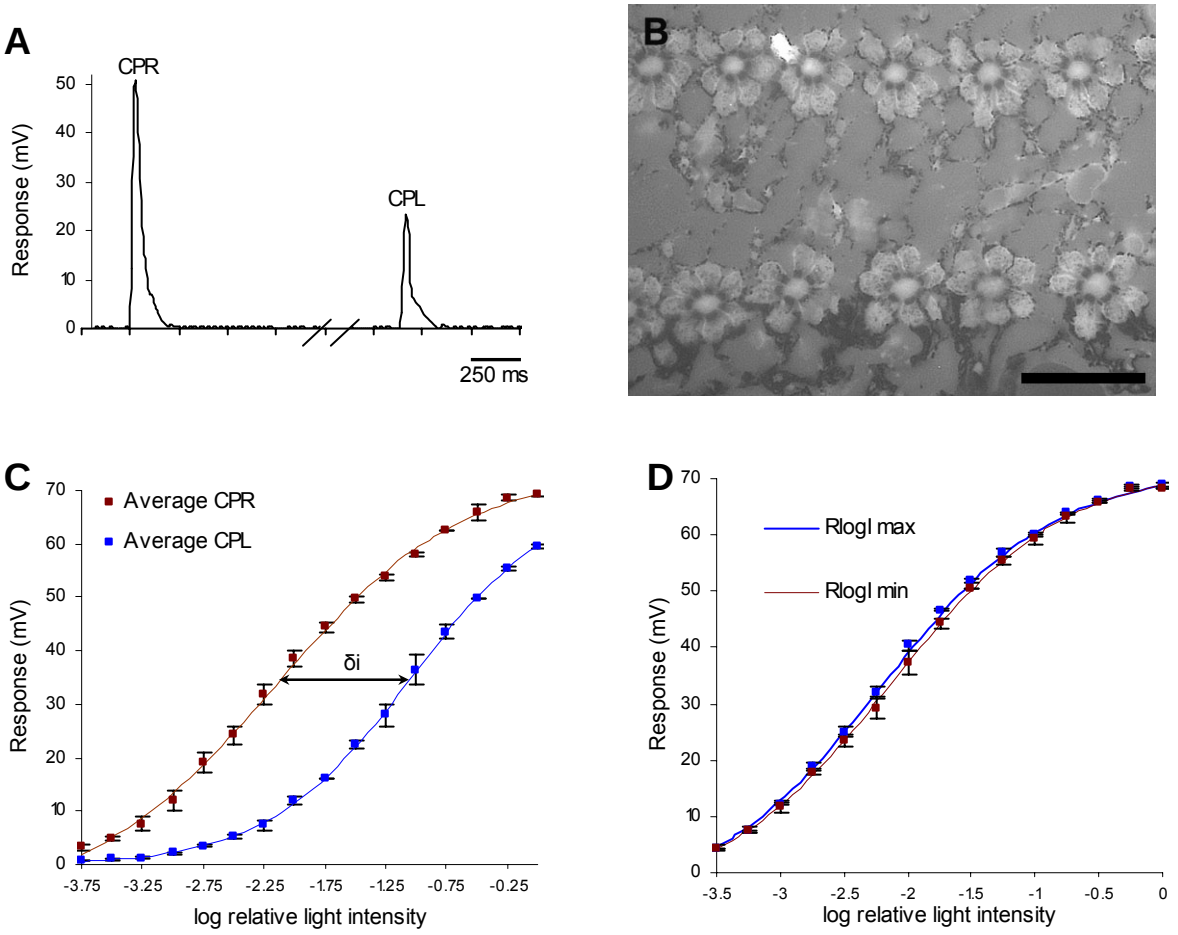


Figure 1 Mid-band row 5&6 R1-R7 photoreceptors are sensitive to circular polarized light

Intracellular recordings from a mid-band row 5 R1 photoreceptor in a right eye of *G. smithii*. (A) Photoreceptor activated with two consecutive 50 ms long flashes of first right-handed (CPR) and then left-handed circular polarized light. This photoreceptor shows a stronger response to right-handed circular polarized light. (B) 7 µm thick frontal section through the retina showing the injected photoreceptor. Scale bar 50 µm. (C) To determine the polarization sensitivity of the cell, two *R*-log *I* functions were recorded (mean ± s.d. *N*=2) using brief flashes of right-handed and left-handed circular polarized light. The intensity shift (δi) of 1.1 log units between the linear parts of the two curves corresponds to a circular polarization sensitivity of 12.59. (D) Most of the photoreceptors R1-R7 within mid-band rows 5&6 showed no sensitivity to linear polarized light. This cell was 1 out of 4 which had a low remaining linear polarization sensitivity of 1.15 (δi =0.062 log units) (mean ± s.d. *N*=2).

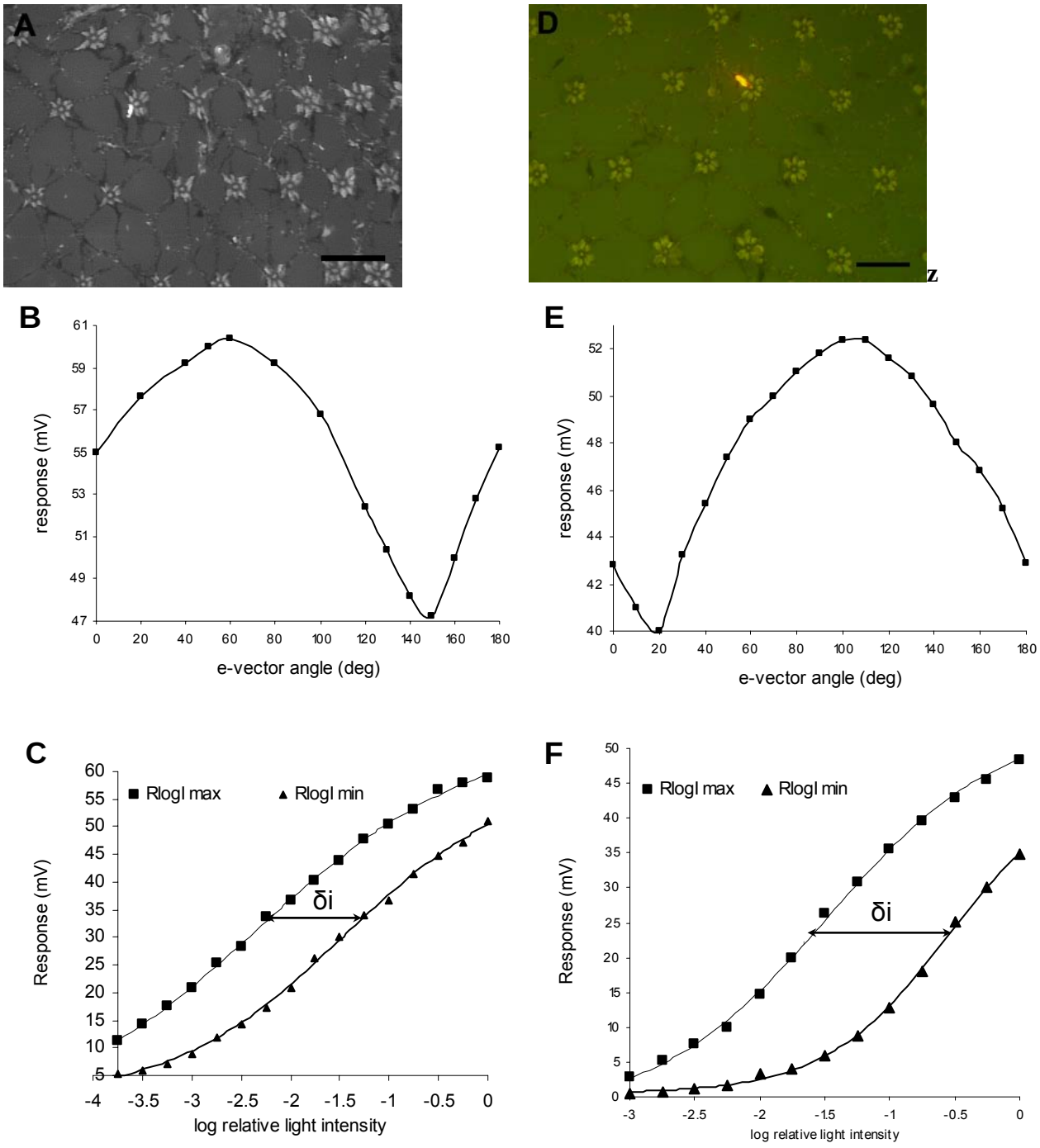


Figure 2 Hemispheric photoreceptors R1-R7 are sensitive to linear polarized light

Intracellular recordings from two hemispheric receptors in a right eye of *G. smithii.* A-C Photoreceptor R1 of the dorsal hemisphere. D-F Photoreceptor R1 of the ventral hemisphere (A, D) 7 µm thick frontal plastic sections showing the stained cells. Both stained cells are the R1 receptors. Notice the 45˚ counter-clockwise rotation of the photoreceptor arrangement in the ventral hemisphere compared to the dorsal hemisphere. Scale bars 50 µm. (B) E-vector / Response function. This receptor is most sensitive to an e-vector orientation of linearly polarized light of 60˚ (Φ_{max}) and least sensitive to an e-vector orientation of 150˚ (Φ_{min}). (C) To determine the polarization sensitivity, two *R*-logI curves were recorded at Φ_{max} and Φ_{min} respectively. In this example, the intensity shift (δi) of 0.975 log units between the linear parts of the two fitted functions corresponds to a polarization sensitivity of 9.43. (E) This receptor is most sensitive to an e-vector orientation of linearly polarized light of 105˚ (Φ_{max}) and least sensitive to an e-vector orientation of 15˚ (Φ_{min}). (C) *R*-logI curves were recorded at Φ_{max} and Φ_{min}. The intensity shift (δi) of 1.024 log units

corresponds to a polarization sensitivity of 10.56. Notice that the microvillar orientations and therefore Φ_{max} are rotated 45˚ to each other between the dorsal and the ventral hemispheres. In total the hemispheres therefore contain four different e-vector sensitivities.

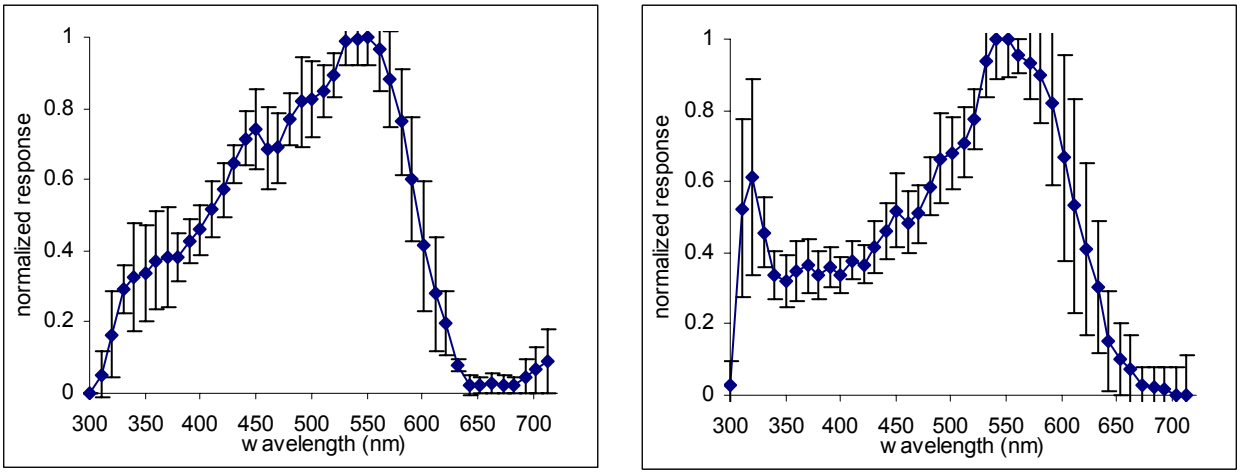
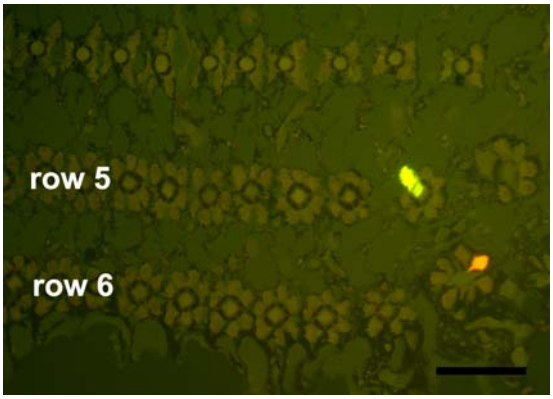
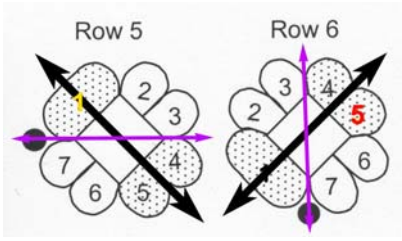


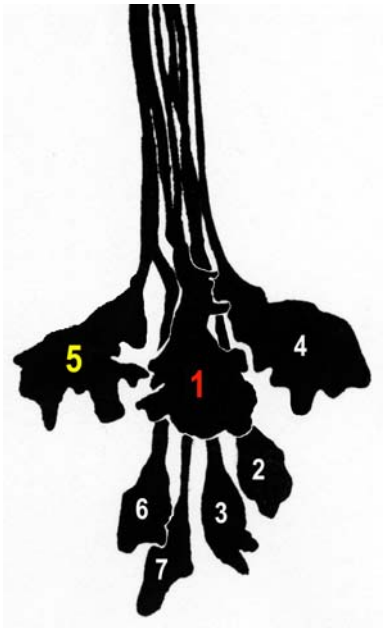
Figure 3 Comparison of the averaged (± s.d.) spectral sensitivity curves of mid-band row 5&6 R1-R7 photoreceptors (left) and hemispheric R1-R7 photoreceptors (right) of *O.scyllarus*. The spectral sensitivities were measured with the spectral scan method where a photoreceptor is clamped to a preselected DC potential by adjusting the light flux during changes in spectral content (Menzel et al., 1986). Mid-band row 5&6 and hemispheric R1-R7 receptors have similar overall sensitivities with maxima at 550 nm. The main difference is the absence of a UV peak in the spectral sensitivity curves of mid-band rows 5&6 R1-R7 receptors (left). This could be due to either 1) the increased filtering effect of the extraordinarily long (150 µm) overlying R8 receptor, which is sensitive to UV-light peaking around 330nm (see figure 6). In comparison, the R8 cells of the hemispheres are only 50 µm long and their spectral sensitivity functions peak at 320 nm or 2) that the R8 cells in the hemispheres are electrically coupled to the R1-R7 cells causing the UV-peak in the R1-R7 cell spectral sensitivity function. The hemispheres are believed to be used for range-finding and motion vision and electrical coupling would increase sensitivity and therefore acuity.



A: 7 µm frontal plastic section through the retina of a right eye of *O. scyllarus* showing two dye-filled circular polarization sensitive cells within mid-band rows 5&6: mid-band row 5 R1 receptor injected with Lucifer yellow (yellow) and a mid-band row 6 R5 receptor injected with Ethidium bromide (red). We recorded from both cells and they were both most sensitive to right-handed circular polarized light. Scale bar 50µm.



B: Diagram of a frontal view of the photoreceptor R1-R7 arrangement in the main rhabdoms of mid-band rows 5&6 in a right eye. The two photoreceptors injected in the section above, mid-band row 5 R1 (indicated as 1) and row 6 R5 (indicated as 5) possess orthogonal microvilli and are therefore sensitive to orthogonal e-vector orientations of light (indicated by black arrows). Because the microvilli of the overlying R8 cells in row 5 are arranged horizontally and in mid-band row 6 vertically (optical axis indicated by purple arrows), the angle between the R8 (retarder) optical axis and the microvillar direction of the cells in both rows is +45˚. Both cells are therefore sensitive to right-handed circular polarized light.



C: Photoreceptor termination pattern in the first optic neuropil, the lamina (Kleinlogel and Marshall, 2005). The termination pattern of the R1-R7 cells within mid-band rows 5 and 6 is identical. The injected cells shown in A are indicated by 1 and 5**.** They both terminate in the outer lamina plexiform layer and connect to the same kind of first order interneurons (monopolar cells). They are both sensitive to right-handed circular polarized light and identical information, in this case about the handedness of circular polarized light, is therefore maintained at the first visual synapse.

Figure 4 Mid-band rows 5&6 R8 cells act as ¼-wave retarders and uniform polarization channels are therefore maintained within the lamina

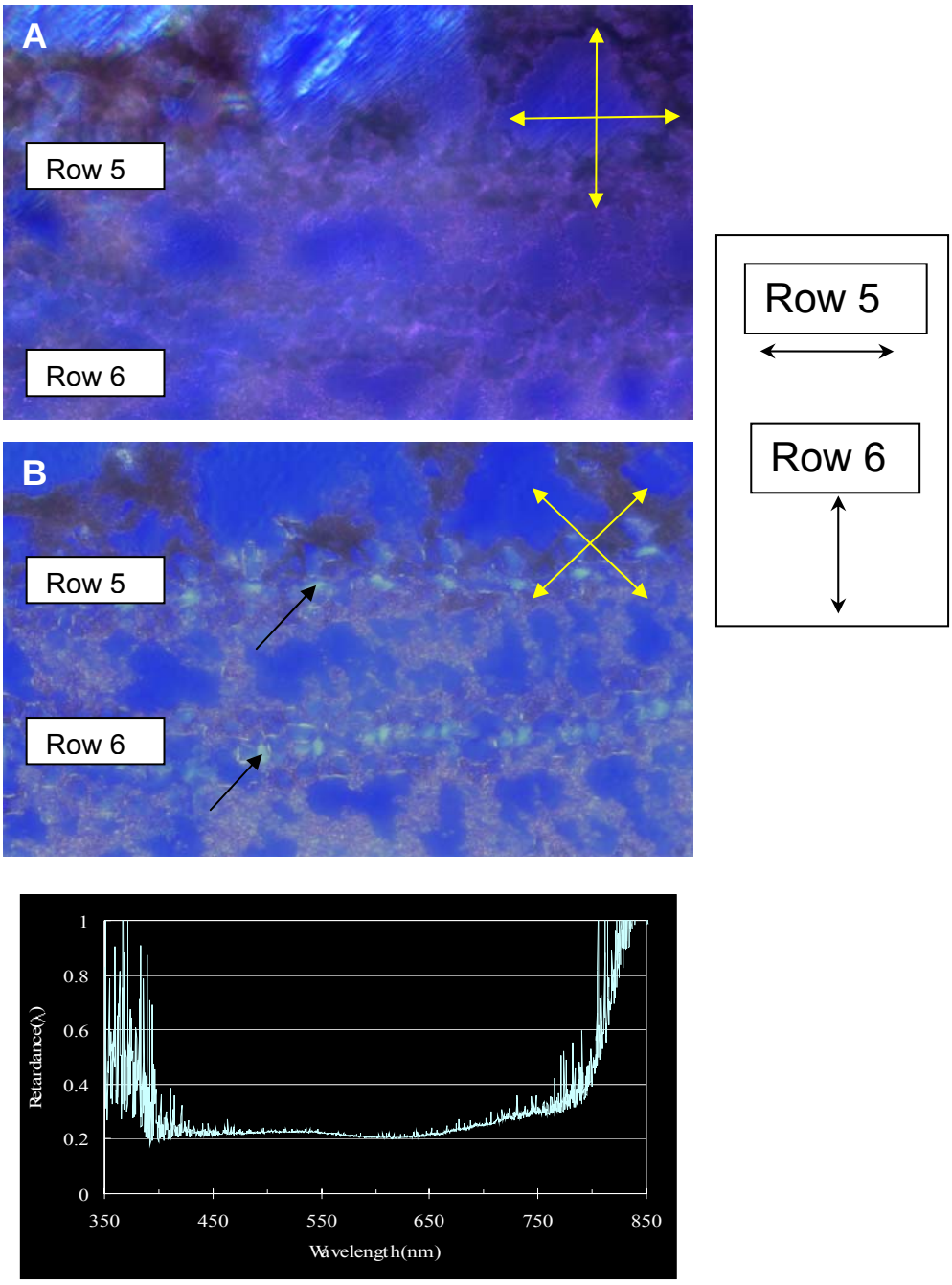
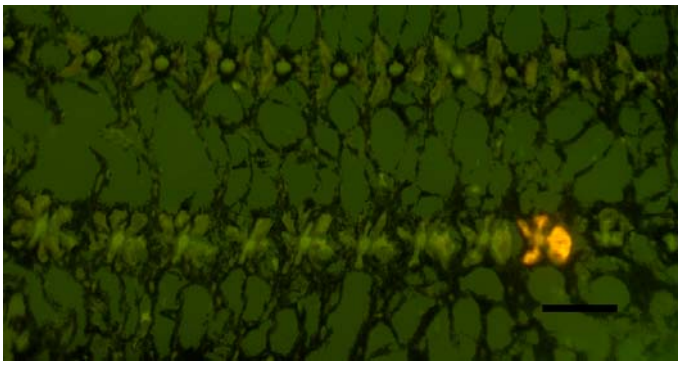
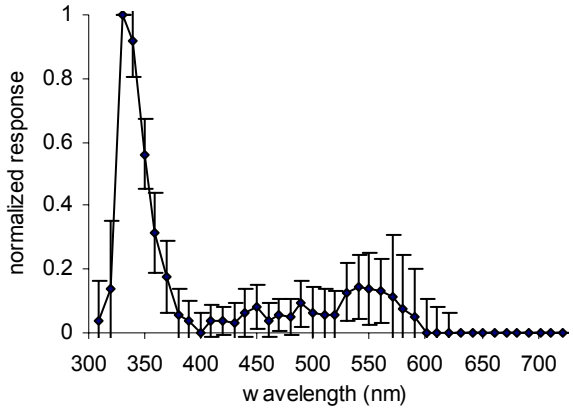


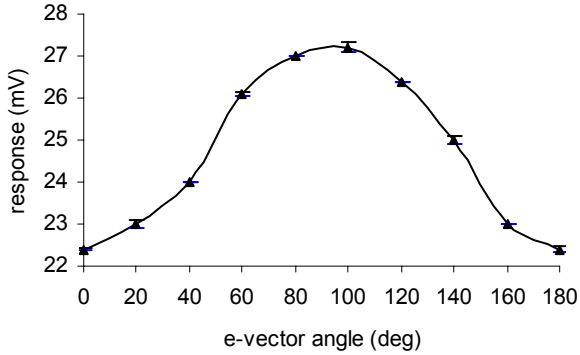
Figure 5 (A, B) Rhabdomeres of mid-band rows 5&6 R8 cells examined between crossed polarizers (polarizer axes are indicated in yellow). The mocrovilli of mid-band row 5 R8 cells are arranged horizontally along the equator of the eye whereas microvilli of mid-band row 6 are arranged vertically. Only when the polarizer axes are arranged at 45˚ to the axis of the R8 microvilli (B) light is transmitted through the rhabdomeres of the R8 cells (black arrows). This indicates that the R8 cells have either ¼-wave or ¾-wave retarder properties. Electrophysiological recordings confirmed that R8 cells act as ¼-wave retarders (see Fig. 4B). (C) Predicted retardance of a 150µm long R8 rhabdomere of *O. scyllarus.* The R1-R7 cells are sensitive to wavelengths between 300 nm and 650 nm (see Fig. 3). In order to work in the spectral range of the retardance of the R8 cell (and the achromatic area of the ¼-wave retarder plate) we used a 400 nm cut-off filter when recording circular polarization sensitivities from mid-band rows 5&6 R8 cells. Pictures by Chiou T-H.



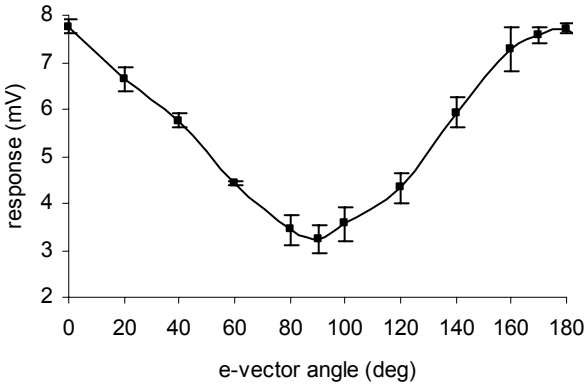
A: 7 µm frontal section through the retina showing the four-lobed R8 photoreceptor in the distal retina of mid-band row 5, injected with Ethidium bromide. Scale bar 50 µm.



B: The averaged spectral sensitivity function (± s.d.) of mid-band row 5&6 R8 receptors. Their peak sensitivity is in the UV at 330 nm.



C: Linear polarization efficiency function (mean +/-s.d., *N*=2) of a mid-band row 5 R8 receptor measured with monochromatic light of 20 nm bandwidth at 330nm. This cell has a maximum sensitivity to an e-vector orientation of 90˚ (:= horizontal), which was predicted from its horizontally arranged microvilli. PS (polarization sensitivity) = 2.73.



D: As C, but for a mid-band row 6 R8 receptor which has vertically arranged microvilli and is therefore maximally sensitive to an e-vector orientation of 0˚ (:=vertical). PS=3.4, mean +/- s.d., *N*=2

Figure 6 The R8 cells of mid-band rows 5 & 6 have a dual function in two separate spectral wavebands: ¼-wave retarders in the green and linear polarization analysers in the UV

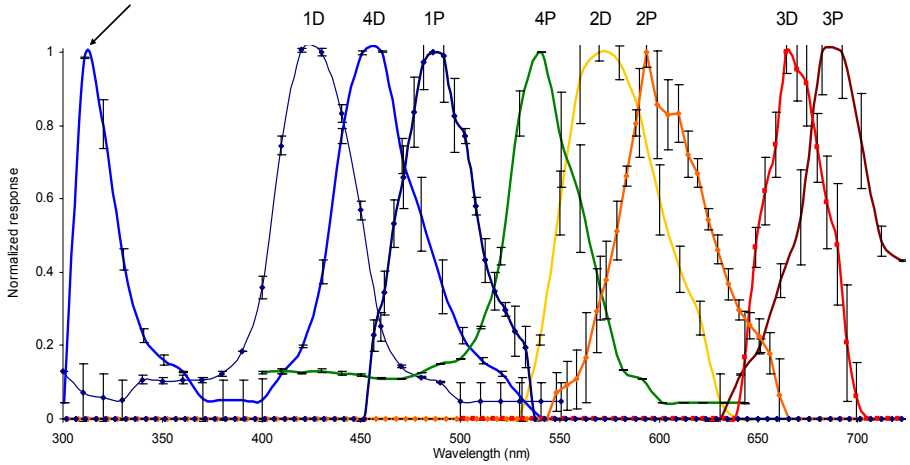


Figure 7 A: The spectral sensitivities (mean ± s.d.) of the R1-R7 cells within mid-band rows 1-4 of *O. scyllarus* measured intracellularly. Electrophysiological measurements are performed on the intact eye, so that filtering effects of all the overlying optical structures are taken into account, whereas previous microspectrophotometric measurements are from absorbance of excised photoreceptor parts (Cronin et al., 2002). Within each mid-band row there exists a pair of narrow spectral sensitivities. From neuroanatomy we assume that colour vision in stomatopods is composed of multiple dichromatic channels. Notice the strong UV-peak of 4D receptors (arrow), which may be either caused by green light emitted from an UV-absorbing pigment in the cornea or from electrical coupling to the UV-sensitive R8 receptor. The spectral sensitivities of other gonodactyloid species (*G. smithii, G. chiragra and H. glyptocercus)* are very similar. *1-4* mid-band row 1-4, *D* distal tier, *P* proximal tier.

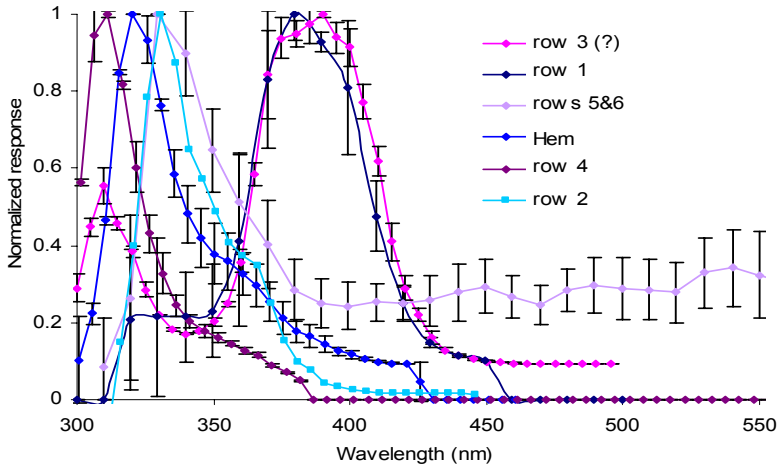


Figure 7 B: We found 6 different UV sensitivities within the eyes of *O. scyllarus* (shown here) and other gonodactyloid species. The double-peaked UV-sensitivity (385nm/310nm) belongs to a mid-band R8 cell, none of which has been stained unfortunately. We assume that the double-peaked spectral sensitivity arises from electrical coupling of two R8 cells, most probably the R8 cell of mid-band row 3 (assumed from a staining that was slightly ambiguous) and the R8 cell of mid-band row 4 (310nm). All other R8 cells have been injected successfully for identification. Note that the spectral sensitivities of mid-band row 2 R8 cells and mid-band rows 5&6 R8 cells are very similar, although mid-band row 5&6 R8 cells also show some sensitivity to visible light.